A STUDY OF TILLANDSIA USNEOIDES.

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(WITH ONE FIGURE AND PLATES VIII–XI)

Tillandsia usneoides, popularly called "long moss," "black moss," or "Spanish moss," is the most widely distributed representative of the tropical and subtropical family Bromeliaceae. According to SCHIMPER (1) it extends from southern Virginia, its northern limit, as far southward as the Argentine Confederation. It forms everywhere a conspicuous and characteristic object of the landscape, its long gray festoons adorning not only trees of the virgin forest but many cultivated ones as well. Although the beauty of the landscape is enhanced by its presence, its growth upon ornamental trees is regarded often with apprehension, a common impression being that it lives parasitically. A most casual examination, however, will reveal the fact that the moss is in no way connected with the tree, but merely wraps its dead, wiry stems loosely around the twigs in order to support itself. Old festoons which have hung in the same place for years occasionally show a connection with the bark, the annual growths of the limb finally enclosing some of the decorticated moss stems; much in the same way that an old horseshoe hung astride a branch and left unmoved for a long time will be partially enclosed.

An indirect cause of the popular belief in the parasitism of Tillandsia is its preference for sunny exposures. This habit would tend to keep it from trees having a dense shade. In dark forests it hangs suspended from the higher limbs of tall trees, especially those that are dead. Many a cultivated tree when in perfectly healthy condition possesses too dense foliage to serve as a host for Tillandsia, but if for some reason the supply of leaves should be reduced, the light conditions might be such as to make the presence of the epiphyte possible. Should it make its appearance, the owner of the tree would be very apt to regard the moss as the cause rather than the result of the reduced foliage. A proof of the true epiphytism of the plant is its long-continued and vigorous growth upon decorticated limbs of dead trees. Near Baton Rouge are many such trees, killed by girdling long ago,

yet supporting a large quantity of moss. In order to demonstrate experimentally that the moss can live solely on what it derives from air and rain, some festoons were supported by twine and hung from some branches of a tree upon which moss was already growing. As was expected, the festoons produced normal flowers, gave rise to new growth, and at the end of eighteen months looked as vigorous as any on the tree, though they came at no time in contact with it.

Because Tillandsia has no influence as a parasite, it does not follow that it exerts none in other ways, yet to just what extent it affects a host tree is at present difficult to say. Aside from the slight damage done in breaking twigs and small branches by its weight, it is doubtful whether such objections as shading and cutting off the supply of air are really worthy of consideration. It is almost certain that these objections are not sufficient to explain a reduction in foliage that people so often ascribe to the presence of the moss. It is realized, however, that this problem can only be answered satisfactorily by experiments extending over a considerable number of years.

The problem of the distribution of *T. usneoides* upon the various species of trees is one of the first to force itself upon the observation. That certain trees of a given locality are abundantly supplied while others not far distant are not, is a well-known fact. One factor in the case has already been mentioned, and that is the light relation. But there are others to be considered, and the most important perhaps is concerned with the method of dissemination. The epiphyte is not usually propagated by seeds but by fragments of festoons, which being somewhat heavy cannot be carried far except in a very high wind, or by birds, which according to SCHIMPER (1) in some regions utilize the plant in building their nests. There is a good chance, therefore, for a tree a little distant from others bearing the moss not to receive its first detachment of the epiphyte.

The character of the foliage also plays a part, in that a tree with leaves densely crowded on the outermost twigs would scarcely permit a wind-blown fragment of moss to hook itself to the branches, but would shed it. SCHIMPER (1) observes in this connection that "Bäume mit sehr dichtem Haube entbehren der Sonnenepiphyten beinahe gänzlich." According to PEIRCE (2) *Ramalina reticulata*, a lichen having a habit and mode of dissemination similar to *T. usneoides*,

is found more frequently on deciduous than on evergreen trees, because, as he explains, the foliage of the evergreen trees interferes with its reaching the branches. The umbrella tree (*Melia Azederach*) has a remarkably dense foliage and is almost universally devoid of moss, yet near the university is a tree of this species with a scanty supply of foliage and an abundance of moss. It is reasonable to conclude that any tree furnishing proper conditions for attachment and growth may become a host of the epiphyte.

The source of the water supply of Tillandsia is atmospheric precipitation, as in all epiphytes. Dissolved in the water are the necessary salts which have been dissolved by the rain from the dust in the air. Perhaps an equally fruitful source of salts is in many cases the washings from the tree, which in dry weather may accumulate much earthy material in the form of dust upon its branches. The plant itself even serves in collecting dust on account of the scaly surface, so that when wet the deposits beneath the scales yield a small amount of soluble material.

A most remarkable characteristic of Tillandsia is its ability to retain water. The absorption of water is accomplished over the entire surface of the living parts by means of scales, as will be described further on, its retention being accomplished also by the scales, and of course by the cuticularized epidermis. It is much easier to understand how a melon cactus with its globose form and consequent minimum surface and enormously developed water-storage tissue can resist prolonged drouth than it is to see how Tillandsia with its small cylindrical leaves, much greater surface exposure, and comparatively small storage facility can, without any water supply, endure drouth. A small festoon was hung in a closed dry room for nineteen days without water. It lost 23 per cent. in weight during the time, but when placed in water it absorbed as much as it had lost, and remained a healthy plant, showing that it had not really suffered injury by exposure to the drouth. There is occasionally, of course, a similar drying process in the open air when drouth occurs. During the dry spell in the spring of 1902, moss plants were known to have been subjected to two months of rainless exposure without injury.

From an economic standpoint, Tillandsia is of some commercial value on account of its mechanical tissue. This forms a central

cylindrical strand composed of reduced phloem and xylem, surrounded by a mass of thick-walled sclerenchyma fibers. When the parenchymatous cortex is removed, the sclerenchymatous axis remains as a tough elastic fiber, which serves as a packing in upholstery. The so-called curing process is a means of eliminating the parenchyma. One method largely employed is that of burying the moss in trenches or pits, allowing it to remain till the cortex is dead and in a condition to be removed easily.

DEVELOPMENT OF THE EMBRYO SAC.

The primordia of the ovules arise on the innermost wall of each loculus of the tricarpellate, superior ovary. By a one-sided growth each primordium becomes bent toward the base of the ovary, developing into the anatropous type of ovule. When the bending has reached an angle of about 90°, the nucellus appears as a hemispherical mass of cells, at the base of which can be seen the beginning of the inner integument. Imbedded under two layers of nucellus cells, the single archesporial cell becomes differentiated in the usual way, by its slightly larger size and greater staining capacity (*fig. 2*). As the ovule increases in size, the nucellus elongates, the outer integument appears, and the archesporial cell enlarges considerably, especially in length. There is no parietal cell formed, but by multiplication of cells the nucellus over the archesporial cell forms an additional layer, making three (*fig. 3*). The archesporial cell is now much elongated, and occupies the central region of the nucellus. It is filled with granular, longitudinally-striated cytoplasm, and has a relatively large nucleus. The first and second divisions of this nucleus probably give rise to the gametophyte generation. Only one spindle of the first division was observed, and it was but little more than one-third the length of the cell (*fig. 4*). The chromosomes were short, and closely crowded at the equatorial plate. The conditions were altogether unfavorable for ascertaining their number on account of the small size of the figure. The number, however, was definitely made out from the second division of the pollen mother cells, and was found to be sixteen. A protracted search failed to yield a nuclear figure which definitely showed the chromosome number in the sporophyte, though considerably over sixteen were observed.

The first division of the archesporial cell is usually followed by a transverse wall and a resting condition of the nuclei (*fig. 5*); but a single case was observed, as reported by SMITH (3) for *Eichhornia crassipes*, in which a row of four nuclei was formed without separating walls (*fig. 7*). In Eichhornia the absence of the walls is said to be the rule, but in Tillandsia it is the exception. The division which gives rise to the third and fourth megaspores, thus completing the axial row, will be seen from *fig. 6* to be in the cell nearest the micropyle. In the meantime, the basal of the two proximal megaspores begins to elongate, and is destined to develop into the embryo sac. A vacuole is formed in this cell as it pushes outwards crushing the other three megaspores, whose contents soon show evidence of breaking down. The remaining stages in development are the familiar ones of complete absorption of the non-functional megaspores by the functional, and the internal division of the latter into eight cells. The two cells that are to form the synergids soon come to possess larger nuclei than does the egg cell. The egg nucleus in fact is smaller than is customarily observed. In the completed embryo sac, the egg often lies against the wall of the sac near one synergid, but may occupy a position between the synergids. The polar nuclei usually approach each other and fuse near the antipodal region (*fig. 14*). The antipodals occupy a pocket at the extreme end of the sac.

FERTILIZATION.

The pollen tube passes through the micropyle, penetrates the nucellus, and enlarges as it enters the embryo sac. It does not appear to pass between the synergids, but to one side of them, one synergid being disorganized in the process. The two male nuclei which have arisen from the generative nucleus during the development of the pollen tube lie near together and a little in advance of the tube nucleus. In no case observed did the male nuclei show the much elongated, spermatozoid-like form so often described for other plants. In *fig. 15*, which represents the tube before its rupture, they are elliptical; but when discharged they are slightly more elongated and may have pointed ends. The place of discharge may be either at the end of the tube or lateral, though near the end (*figs. 16–19*). The tube nucleus is usually to be seen at the time of dis-

charge of the male nuclei, but may be absent later, which would indicate that it too was ejected. In one instance (*fig. 19*) the nucleus was observed after ejectment. The male nuclei are of about the same size and appearance, and leave the pollen tube at about the same time. The nucleus which is to fuse with the endosperm nucleus can be seen in various stages of its passage to the antipodal end of the embryo sac. There is no evidence that either nucleus increases in size after leaving the pollen tube. The time of fusion with the polars may be either before or after their complete union with each other; in *fig. 18* it is before. In *fig. 18* the fusion of the two male nuclei with the egg and polar nuclei respectively is seen to be simultaneous. After fertilization the egg secretes a wall about itself and rests for a time.

The occurrence of darkly-stained bodies so frequently seen in pollen tubes has been noted in Tillandsia. They were observed in the microspores before germination, which would account for their presence in the pollen tube.

THE SEED.

The most noticeable change that results from fertilization is the extensive elongation of the entire ovule. Part of the growth is due to enlargement of the embryo sac and its surrounding integuments, while the remainder is traceable to elongation of that part of the outer integument which is prolonged above the body of the ovule. The inner integument does not appear to elongate at all, hence the opening of the micropylar canal comes to lie far below the opening of the canal formed by the outer integument (*fig. 22*). A similar elongation of the outer integument was observed in *Puya chilensis* by HOFMEISTER (**4**).

Accompanying the growth of the embryo sac is the development of the endosperm. It begins to form at once after fertilization, and the nuclei resulting from the first divisions of the endosperm nucleus take position at either end of the sac, leaving, however, a few to form a thin parietal layer between. At the antipodal end, cell formation with walls begins at once, and a number of large cells form a tissue which stands out conspicuously in the cavity of the sac, which otherwise contains only a few free endosperm nuclei. At first this tissue

was taken as an extraordinary development of antipodals, but cases were found where the three degenerate cells were lying beneath the tissue in the small pocket at the end of the embryo sac. The free endosperm nuclei gradually gather in increasing numbers against the endosperm tissue, finally forming walls about themselves but remaining readily distinguishable from the other tissue (*fig. 24*). The functions of the two tissues appear to be somewhat different. The originally formed cell-compact retains its richness of protoplasmic contents during the development of the embryo, probably serving in the conduction of food materials to the later formed tissue adjoining it, which soon shows signs of containing food deposits. The reserve materials thus laid down are not utilized by the embryo before seed germination, but exist as the endosperm of the ripe seed. The endosperm at the micropylar end of the embryo sac does not develop in large quantity, forming a tissue about the embryo only after the latter attains a considerable size.

The egg cell remains dormant for a time after fertilization. In 1903 the period of blossoming lasted (at Baton Rouge) for a month following the middle of May. Material gathered about the first of July showed egg cells undivided, as well as embryos of only a few cells. Growth during the summer is slow, small embryos being found in material gathered about the tenth of August. It was not till the middle of September that large ones were observed, and even then there was much diversity in size.

The first wall formed in the division of the egg cell is transverse, as is the second one also. The proembryo of three superimposed cells is therefore not different from the type that holds in so many monocotyledons. The divisions immediately following, however, vary considerably in sequence.

The middle segment may divide sooner than the terminal (*fig. 28*), or the reverse may be true (*fig. 27*). The basal segment divides sooner or later by longitudinal walls into four cells—a variation from the Alisma-type, in which the segment is unicellular and vesicular. The terminal segment divides by longitudinal walls to form the quadrant, and by transverse walls to form the octant. The latter walls instead of being precisely transverse may be oblique (*fig. 34*). In many older embryos the arrangement of the cells in this segment

indicates that the walls in question were originally oblique or else became so by unequal growth in different parts of the embryo (*fig. 36*). The dermatogen usually forms first in the terminal segment. To distinguish the middle from the terminal segment soon becomes a difficult matter, but from the position of the concavity in which the stem apex is developed, it is safe to say that the apex arises from the middle and the cotyledon from the terminal segment, as in Alisma. The middle segment also gives rise to the root-tip, hypocotyl, and part of the suspensor. A short time before the differentiation of the stem tip in the lateral depression, the region adjoining and outside of the area where the stem tip is to appear grows upward into a ridge of tissue, which in the mature embryo encloses the growing point completely. If the figure of the embryo of Guzmannia, as shown by WITTMACK in Engler and Prantl's *Natürlichen Pflanzenfamilien* be compared with that of *T. usneoides* (*fig. 40*), the resemblance will at once be apparent. It will be noticed that what I have called cotyledon in Tillandsia is called scutellum in Guzmannia, the term cotyledon[1] being reserved by WITTMACK for the small outgrowth labeled *c*, near the stem apex. It is probable that the author in thus naming the two organs scutellum and cotyledon only wished to emphasize the difference in function, one as an organ of absorption, the other as a rudimentary leaf, at the same time recognizing the two as homologous with the cotyledons of the dicotyledons. From a study of the seed germination of *T. usneoides*, however, it will be seen that it is extremely doubtful if the organ named cotyledon in Guzmannia is really such. Further discussion of this point, however, will be postponed till seed germination is considered.

When the embryo of Tillandsia is about three-fourths grown, there occurs a degradation of certain cortical cells of either the root or the end of the hypocotyl nearest the root-tip. The cells in question show at first a contracted protoplast, with incapacity to stain deeply, and by the time the embryo has reached its full size almost a complete absence of cell contents (*fig. 42*). This phenomenon undoubtedly stands in intimate relation with the complete atrophy of root that obtains in the mature plant.

[1]The index letter *c* in the description of *fig. 19*, *G* of the Bromeliaceae has been found through correspondence to indicate cotyledon.

Dispersal of seeds in the Tillandsia is accomplished by the assistance of long delicate hairs that beset the seed coat. These arise by elongation of the cells of that part of the outer integument which forms a portion of the body of the seed, and also from that part which extends to the funiculus. The hairs not only assist in wind transportation, but are also of use to the seed in enabling it to adhere to bark or festoons of moss. The adaptation for effective adherence consists in closely appressed barbs attached to the hairs at intervals (*fig. 44*). Soon after the opening of the capsules, numerous instances of seeds clinging tightly to limbs and to moss festoons may be observed.

The time of discharge of seeds is in March (at Baton Rouge). I have no data as to possible variation of this time in localities widely distant, but suppose it is nearly uniform for the southern states. March, of course, is an unusual month for dehiscence of fruits in the north temperate zone, but in Tillandsia it stands in close relation to another property not generally possessed by seeds in temperate climates, that is, quick germination. Though lack of facts forbids positive statement, it may be conjectured that this relationship originated from ancestors living in tropical lowlands, where a dormant period to withstand unfavorable conditions is unnecessary.

GERMINATION OF THE SEED.

Tillandsia produces seed in considerable quantity each year. Just what proportion contains fully-matured embryos has not been ascertained, but there is no doubt that a large percentage have them. The embryos appear perfectly normal, with the exception of the dead cortical cells in the root or hypoctyl, and show no apparent reason why they should not give rise to seedlings. The experience of investigators, however, has been that seeds produced by the epiphyte are worthless, a condition which has arisen through the introduction of a vegetative mode of reproduction, whereby seed-production has degenerated. Nevertheless, I made efforts to induce seeds to germinate by placing them in a germinator, but without success. MEEHAN (**5**) reports having found the seed germinating in the hollow crotch of a tree in which vegetable mold had collected. He says that from the seedlings or young plants proceed stolons or runners, having buds

every few inches, which push out into leaves and stems to form the gray-green moss. SCHIMPER (1) succeeded in finding one seedling, but he gives no description of it. MEZ (6) states he was unable to obtain any seedling at all. Realizing that the observations of MEEHAN were worth consideration, I searched crotches of moss-laden trees, in which plenty of vegetable mold had collected, but without success.

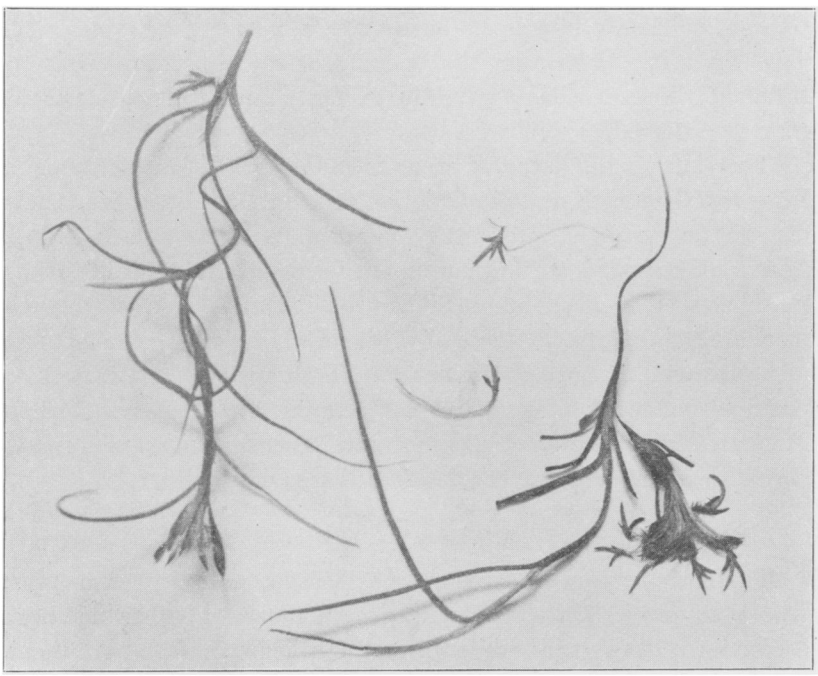

FIG. 1.—Seedlings of *Tillandsia usneoides;* on the right is a cluster of seedlings still attached by their coma to a partially opened capsule; near the top of the shoot on the left a seedling is adhering to the scaly surface.

I then planted seeds in the mold, but they could not be induced to germinate. On April 6, 1903, I observed Tillandsia seedlings for the first time, and they were projecting from a partially-opened capsule (*fig. 1*). Out of the nineteen seeds in the capsule, thirteen had developed into seedlings. They were held in place by the tuft of hairs from the testa to which they still adhered. An examination of moss festoons was then made, with the result that many little

seedlings were found either still attached to the capsules, or else hanging to the scaly stems and leaves of the mother plants. In every case the seed coat still adhered to the base, or root-end of the seedlings, so as to enable the coma to keep them from falling to the ground, which they certainly would have done without this provision. When it is remembered that the capsules dehisced in March, and the seedlings were found early in April, it will be seen that germination followed dehiscence quite closely. Of course the early growth was attained at the expense of the endosperm, but when it was exhausted, continued growth, which would naturally be expected from healthy looking seedlings, failed to occur. Material gathered in the summer and autumn yielded the usual crop of seedlings, but in no case were any found that were larger than those found in April. Festoons gathered the middle of January, nearly a year after the capsules opened, had numerous little seedlings hanging to them, all healthy looking, but no larger than any observed before them. It is expected that when the warm weather of spring comes, when Tillandsia puts forth its most vigorous growth, the seedlings also will increase in size. The question naturally arises here, why Tillandsia seedlings are not to be seen in all stages developing into mature plants, counting of course those which germinated previous years. As such is not the case, it can only be conjectured that, as the spring of 1903 was an unusually rainy one, the conditions for germination were especially favorable.

Seedlings exhibiting various stages in germination were imbedded in paraffin and longitudinally sectioned. In the earliest stage (*fig. 45*) the first leaf shows only a slight growth, the stem apex is still undifferentiated, while from the axil of the ridge of tissue that enclosed the stem apex, or else from its inner surface, a pair of organs have arisen. It is believed that the presence of these organs throws some light upon the morphological nature of the ridge of tissue. If a section is made through the nodal region of a mature plant (*fig. 49*), it will be seen that the leaf sheath which encloses the lateral shoot and main axis is double. The doubling is not due to splitting of a tissue once entire, but to bifurcation. A section through a very young sheath (*fig. 49a*) reveals an outgrowth, one to several cells in extent, from which a double layer of cells arises. These soon separate to

form the double sheath. In older stages the base of the sheath is composed of many cells in width, so that the sheath appears no longer to originate as a bifurcation of a single organ, but rather as two distinct organs. Both organs or portions of the sheath may develop equally, though it more often happens that one portion becomes larger than the other. Occasionally, the inner scarcely develops at all, but remains a tiny rudiment.

The sheaths which arise in the seedling develop precisely like those in the mature plant and differ from them in no respect. The two organs that originate on the ridge of tissue, therefore, may be regarded without hesitation as the first sheath, and as every sheath appears in connection with a leaf, that leaf must be the cotyledon. From the section of the mature plant it will be noticed that the bases of each leaf and its sheath are at the same level on the axis. If a difference in level should occur, however, whereby the base of the sheath were elevated above that of the corresponding leaf, the cell growth producing that elevation would originate from the cortical parenchyma lying immediately under the sheath. The parenchyma would give rise to a ridge bearing the sheath upon its summit. Such an occurrence does not of course actually take place in the mature plant, but it is believed that it is in such a way that the ridge of tissue originates in the embryo. Reasons for coming to this conclusion are based upon the position of the first sheath. While the inner portion of the sheath may grow from the crotch at the base of the ridge of tissue, the outer, and sometimes the inner also, is attached to the ridge upon its inner surface. The outer portion may in fact arise from the summit of the ridge. The base of the sheath, therefore, is on the whole raised above that of the cotyledon, the elevation being accomplished through growth of the subjacent parenchyma. Thus there develops a special organ which serves a special purpose, perhaps as protection to the stem apex, and which must therefore be regarded as an embryonic structure without an exact counterpart in the adult plant. It cannot be a leaf, or a cotyledon, because a leaf does not bear such a relation to its sheath. A leaf and its sheath always develop with a growing point between them, so that they can never join in a median section. CAMPBELL (**7**) calls a similarly placed though less extensive outgrowth in the embryo of Sparganium a sheath. While it does not require a

stretch of the imagination to consider the growth in question a sheath, there is at least one objection to this solution of the problem. The development of the sheath shows that it appears as a bifurcated organ almost from its incipiency, and that the base, at first narrow, subsequently increases greatly in width. Quite the reverse would be true in the embryo if the organ enclosing the growing point were regarded as a sheath, for the basal portion is first enormously developed, leaving the upper bifurcated portion to appear comparatively late.

The stages in germination are shown in *figs. 45–48*, which should be compared with *fig. 49*. The latter exhibits a difference in relative time of differentiation of stem and leaf apex as compared with the seedling. In the mature plant the leaf is still quite small when the stem apex becomes distinguishable at its base, while in the seedling the leaf first attains considerable size.

THE FLOWER.

The flowers, which are produced in considerable quantity in May and June, present little of special interest. Each flower has a calyx of three sepals, and a corolla of three green petals. Having a fragrant odor, it is possible that it is visited by insects, though no information has been collected by me on the subject. Thrips, however, inhabit many of the flowers and puncture the style in order to deposit an egg at its base. It is possible, therefore, that they may serve in cross pollination.

Although the flower appears to be terminal, it is regarded by MEZ (**6**) as a reduced indeterminate inflorescence. An examination of preparations made longitudinally through buds bears him out in his statement, for a growing point of considerable size is present, though having dead meristem tissue.

THE LEAVES.

The leaves of *T. usneoides* are acicular and with an approximately semicircular cross section. The epidermal cells do not have specially heavy walls, nor are the inner ones thicker than the outer, as in certain other Bromeliaceae. Sections through the leaf show it to have three fibrovascular bundles, each surrounded by a tissue composed of thick-walled sclerenchyma fibers (*figs. 50, 51*). The principal portion

of the leaf is composed of parenchyma cells which do not show any differentiatiation at all into palisade and spongy tissue. While the cells have the shape of those in typical spongy tissue, the large intercellular air spaces characteristic of most mesophytic leaves are here replaced by small ones, giving the whole tissue a much more compact appearance. Not all of the parenchyma cells contain chloroplasts, for there are interspersed cells without them, whose function is that of water-storage, having walls provided with large pits which facilitate the passage of water from one cell to another.

Aside from acting in the capacity of mechanical tissue, the vascular system has undergone a process of degeneration. The necessity for a functional xylem with its transpiration stream is eliminated by the fact that there is a complete absence of roots, and also by the fact that the water-absorbing organs, the scales, are found over the entire exposed surface with the exception of some of the floral organs. There would appear also to be no need for a functional phloem since all living cells either contain chlorophyll and are exposed to light, or else are approximate to those containing chlorophyll.

THE CHLOROPLASTS.

One of the most interesting features of the leaf is the structure and behavior of the chloroplasts. These bodies, instead of exhibiting the more or less homogeneous structure observed in most chloroplasts, are seen to be composed of masses of smaller chloroplasts, measuring about 2μ long and about a third as wide (*fig. 52*). While a very few cells in every cross section of the living leaf contain chloroplasts of the usual type, the vast majority of them contain such as have been described above. The little chlorophyll bodies have almost, if not quite, the minuteness of bacteria, and for convenience will be spoken of as *microchloroplasts;* the larger bodies, of which they appear to form a part, being distinguished as *megachloroplasts*. The true significance of the formation of the microchloroplasts will be readily seen when it is stated that they may not remain in bunches (*fig. 52*), but can and often do separate from one another till the entire cytoplasm of the cell becomes dotted with them (*fig. 53*). Under a low magnification such a cell appears uniformly green throughout. They even enter the vacuoles, where a lively Brownian movement is set up.

It was at once suspected that the various phases in distribution of the microchloroplasts were conditioned by the light intensity, and hence their movements could be made subject to control. Festoons of Tillandsia accordingly were placed under different conditions varying from darkness to direct sunlight. Those placed in darkness were allowed to remain there 24 to 30 hours, and a similar period of exposure was allotted to festoons hung in the shade. Those exposed to direct sunlight were hung up early in the morning. All were examined during the hours between 11:30 A. M. and 3:00 P. M.

The examination was made by sectioning numerous leaves of various ages, and from as many different regions of each festoon as possible. Plants were also sectioned at different times of day and also at night. The results in every instance were approximately the same. Sections were obtained from plants under the varying conditions of light intensity used in the experiment; sections in which the megachloroplasts were present; in which they were in the process of disintegration into microchloroplasts; in which there was distribution of the microchloroplasts uniformly through the cell; and in which all the foregoing stages were present in the same section. In fact, the same leaf varied in these respects in its different portions. There seemed to be no method of telling before examination just what condition the chloroplasts would be in. One of the best instances of complete uniformity of distribution of the microchloroplasts throughout the cytoplasm was obtained from the tiny leaf of a seedling. That the disintegration of the mega- into microchloroplasts is not the result of injury due to sectioning may be proven by an examination of the entire leaf through the epidermis. Sections also cut thick contain in their centers cells untouched by the razor.

Homogeneous chloroplasts of the usual type were found which showed evidence of undergoing division. Megachloroplasts, in which the microchloroplasts were distinctly visible, were also found showing a deep constriction as though they too were undergoing fission.

Owing to the difficulty of observing well the interior of the leaf through the overlapping scales, it was not ascertained whether the microchloroplasts return to form megachloroplasts or not; but if so it seems certain that the latter would not be constructed of identically the same microchloroplasts a second time.

It is offered in explanation of this interesting condition of affairs that the supply of light of Tillandsia is considerably diminished by the presence of the overlapping scales, which are necessary for water absorption and for protection against too rapid transpiration. In order to meet this diminution, it not only prefers sunny exposures, but has modified its chlorophyll-bearing apparatus by causing it to occupy a much larger area in order to utilize to better advantage such light as penetrates to the interior of the leaf.

It may be stated here that precautions were taken to examine healthy festoons removed directly from moss-laden trees. In some instances these were examined immediately after such removal, lest confinement in the laboratory should in some way induce pathological conditions.

THE SCALES.

The scales cover the entire living exposed portion of the plant with the exception of the corolla, stamens, ovary, and a portion of the calyx. Each scale develops from a single epidermal cell, the early divisions of which occur while the young leaves and stems are included within the leaf sheath. The first division is transverse (*fig. 55*). The proximal cell thus produced remains undivided, the distal dividing transversely till four cells are produced, of which the lower three form the stalk of the scale (*fig. 57*). The outermost hemispherical cell becomes divided into four cells by two longitudinal walls perpendicular to one another (*figs. 58* and *63*). By periclinal walls a central group of four cells becomes separated from four outer ones (*fig. 64*). The central cells divide no further. The outer ones divide by periclinal walls to form two concentric rows (*fig. 65*). The cells of both rows become eight in number by anticlinal walls, the inner row undergoing no further division, but the outer, by another set of anticlinals, finally has sixteen. A fourth concentric row is then formed by periclinal walls from the outermost sixteen cells. The three inner layers consist of four, eight, and sixteen cells respectively, which numbers remain constant, but the fourth layer undergoes repeated divisions till a large number of cells are produced (*fig. 67*). These last lengthen greatly and form the wing of the scale. The surface view of the mature scale is seen in *fig. 68*, the longitudinal section in *fig. 70*. All of the cells but the stalk cells and the original

basal cells undergo thickening of their walls in certain portions and lose their cell contents.

SCHIMPER (1) was the first to call attention to the water absorptive function of the scales, and his experiments along this line were so complete as to leave little else to be done. That the leaves of Tillandsia can absorb water is easily demonstrated either by wetting them with water and then watching it disappear, or by noting the weight before and after allowing them to remain a short time in water. That the channel of absorption is through the scales is shown by using colored water, which stains the stalk cells. Unlike most similar appendages of the epidermis, the scales do not hinder the leaf from becoming wet, but actually conduct water into the interstices beneath them. When dry, the leaf is of a gray color, due to the air enclosed by the scales, but when wet, the air is replaced by water, and a deep green color results. From an examination of *fig. 70* it will be seen that the outer walls of the scale are thickened. When water is absorbed by the cells with thickened walls, they become turgid, expand below, and raise the wing of the scale well above the epidermis (*fig. 69*). The water absorbed by the outer cells of the scale passes to the stalk cells, which have thin walls and rich protoplasmic contents. Through these it passes through the basal cell to the water-storage cells of the parenchyma. If the plant be soaked in dilute potassium iodid solution for a day, the walls of the stalk, basal, and neighboring parenchyma cells will be stained. It should be noticed that no ordinary type of epidermal cell with its thickened cuticularized wall separates the scale from the parenchyma. The cell that represents the epidermis beneath the scale is the basal cell resulting from the first division of the epidermal cell that gave rise to the scale. The walls of this basal cell are thin and uncuticularized. If a scale whose wing is raised well above the epidermis by the turgescence of its cells be treated with glycerin, the contraction due to loss of turgescence will draw the scale close down against the epidermis. This illustrates the process that takes place when scales become dry from evaporation, as occurs in nature. Such a process cannot but assist the epidermis in checking transpiration, so that the scales may be considered not only as organs of absorption, but as serving to prevent too rapid escape of the water they have been instrumental in bringing into the plant.

The effect of an absorptive system extending over the entire surface has already been mentioned in the reduction of the mechanical and conductive tissues. As such reduction is found mostly in submerged hydrophytes, it will be seen that *T. usneoides* behaves in these respects much like such plants.

The scales stand in connection with the water-storage tissue. The cells of this tissue lie well distributed among the chlorophyll-bearing cells and keep them in a state of turgescence. Even after a plant has lost one-fourth of its weight by transpiration, and the leaves have become grooved by contraction, the chlorophyll-bearing parenchyma is unhurt. It is believed that the leaf shrinkage is due to a partial collapse of the storage tissue upon loss of water, rather than by decrease in turgescence of the green parenchyma. There is no evidence that the plant undergoes desiccation and subsequent revival, as in the case of *Polypodium vulgare*.[1]

THE STOMATA.

In addition to protection afforded by scales, hairs, and thick-walled epidermal cells, xerophytes sometimes guard against too rapid transpiration by means of the position and structure of the stomata. Sunken stomata, or those vestibuled by an epidermal air space, itself with a narrow opening to the exterior, are all well known. In some xerophytic plants the usual closing of the pore by the guard cells is assisted in its function of checking transpiration by modifications in neighboring parenchymatous or epidermal cells. In *Kingia australis*, for instance, there is, according to TSCHIRCH,[2] a large intercellular space adjoining the stoma, partially filled with coiled cellular

[1] Since this paper went to press, one by MEZ (**9**) has appeared on the physiology of water absorption in certain species of Tillandsia, among them *T. usneoides*. MEZ corrects SCHIMPER'S observations as to the details of the absorptive process, claiming that the empty cells of the scale do not contain air, but are collapsed when the surface of the plant is dry. The thickened part of the scale swells when wet, raising it and causing the lumen to reappear in the collapsed cells. Water passes from exterior capillary spaces into the partial vacuum through thin places in the cell walls, whence, from the filled cells as reservoirs, the water is taken up and passed into the mesophyll by the stalk cells (*Aufnahmezellen*) through the usual process of osmosis. MEZ describes the scale of *T. usneoides* as having only one stalk cell instead of three. While it is true that two of the cells are very thin, their presence can readily be made out in good sections of mature scales and still more readily in sections of young ones.

[2] HABERLANDT, G., Physiologische Pflanzenanatomie. 2d ed. p. 399. 1896.

outgrowths of the parenchyma. The outgrowths do not stop, but merely hinder transpiration. *Xanthorrhoea hastilis* exhibits a similar contrivance. *Camellia japonica* and *Prunus Laurocerasus* have the faculty of filling up the air space as a result of excessive drouth or by death of the guard cells. In such cases tylose-like processes occur which block up all gas interchange. *Pilea elegans* differs from those mentioned above in that certain subjacent parenchyma cells develop thickenings on their exterior walls. One of these finally pushes up against the pore of the stoma and effectually closes it. There is no movement of the parenchyma cell away from the stoma, hence the aperture is permanently closed. From an examination of *figs. 72* and *73* it will be apparent that Tillandsia presents a condition of affairs not widely different from that of Pilea. The principal difference lies in the fact that in Tillandsia the parenchyma cells undergo no thickening. Both longitudinal and cross sections through the leaf show outgrowths from the parenchyma cells lining the sides of the air space. The outgrowths turn upward and either stop up the opening of the stoma or else press directly against the guard cells. It will be seen that the enormously thickened walls of the guard cells preclude a possibility of change in their form. To show this experimentally some plants were placed in water and exposed to direct sunlight for a few hours. The leaves were then sectioned and the guard cells watched with a micrometer while glycerin was run under the cover glass. There was no measurable change. According to MEZ (**6**) the guard cells have lost the power of functioning, this power having been transferred to certain cells of the subjacent tissue which operate the passive guard cells, thus opening and closing the stoma. There are two cells which come in contact with the guard cell and may therefore be the means of moving it. One is the cell to which it is attached and which extends from the hinge to the inner face of the guard cell. This cell is usually continuous, but may be divided by a cross wall into two cells. Should this cell, which is epidermal, become turgescent, it would tend to raise the guard cell, swinging its free side outwards. Such a movement, however, would close rather than open the pore of the stoma. The hinge is quite thick and may be much thicker than any shown in the figures. If the epidermal cell is divided the division wall would effectually hinder any movement of

the guard cell. From these two considerations it would appear doubtful whether the guard cells move at all in either direction. Of course the glycerin experiment was repeatedly tried, but no motion was discernible. The only other cells which by contact with the guard cells can move them are the parenchyma cells whose processes push against the guard cells on the under side. It was at first thought that the parenchyma cells were operated by variations in turgescence of the epidermal cell, so that regarding the guard cells as immovable the epidermal cell would press downward upon the subjacent parenchyma cell during turgescence, and lower the process, thus unstopping the stoma. Out of a number of such processes only one reaches the center of the stoma, all the others being considered attempts that from necessity have failed. This explanation of the function of the parenchymatous outgrowth is plausible, to say the least, but it has not been experimentally proven by the glycerin test. Numerous instances were investigated carefully, but in not a single case did any of the processes change their position. It is here confessed that no reaction was noticed in any part of the stoma or adjacent tissue in response to the action of glycerin, nor was an instance found in fresh material where the guard cells appeared to be separated. The experimental demonstration of the presence of a mechanism in the stomata, therefore, has not thus far met with success.

Another explanation might be mentioned, in which the processes are to be considered attempts on the part of the plant to close the stomata permanently. It may be that not all the processes actually reach the center of the stoma and close it, so that, granted that a small opening exists between the guard cells, the number of functional stomata would merely be reduced. The total number of stomata per square millimeter was ascertained and found to be relatively small. The estimate was made by counting the number of stomata in each section of serial sections taken from a portion of leaf of known length. For instance, a piece of leaf 3^{mm} long contained 52 stomata. Calculating the surface from the circumference of the cross section, there would be 7 per square millimeter, or, in round numbers, 4,300 per square inch.

It must of course be taken into consideration that *sections* of living leaves were used for experiment and not entire ones. If variations in

the pressure of the water-storage tissue exert any influence on the opening and closing of the stomata it is very probable that the injury done to the tissue in sectioning would greatly interfere with the action of the mechanism.

HABERLANDT (8) figures the stoma of *Tillandsia zonata*, which in respect to guard cells, and their supporting cells, resembles that of *T. usneoides*. The guard cells have greatly thickened walls, and a thickened hinge. From Haberlandt's account it is evident that he does not fully comprehend the mechanism. In *T. zonata* no subjacent parenchyma is mentioned as taking part in the opening or closing of the stoma.

THE STEM.

Aside from the vascular region, the stem differs in no essential particulars from the leaves as to structure. The stem, of course, has the added function of support, so that there is developed between and around the bundles a thick tissue of sclerenchyma fibers (*fig. 74*). The fibers measure about 750μ in length. They do not impart rigidity, but flexibility and power to resist longitudinal strain. If a fragment of moss is blown from one limb of a tree to another, and succeeds in getting a hold, the cortex of that portion of the stem that passes over the limb dies, and then disintegrates, leaving the sclerenchymatous axis, which holds the plant in place for several and perhaps many years. It is upon the durability and elasticity of this tissue that the economic value of the moss in upholstery depends.

What has already been said in regard to reduction in the function of the xylem and phloem of the leaves could with equal truth be said about the stems. With a superficial absorptive system and no root, the xylem as a conductive system is useless. The pendent habit and method of dissemination are both closely associated with reduction in mechanical tissue, though they are more likely to be the result than the cause of the reduction. The parenchymatous cortex, as in leaves, is supplied with chlorophyll-bearing cells, all of which are exposed to light, so that a tissue like the phloem, to carry elaborated materials to cells distant from the center of photosynthesis, would be unnecessary.

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EXPLANATION OF PLATES VIII–XI.

FIG. 2. Ovule fundament showing archesporial cell.

FIG. 3. Young ovule at period just before first division of archesporial cell.

FIG. 4. Spindle of first division.

FIGS. 5–6. Stages in formation of axial row of potential megaspores.

FIG. 7. Megaspores without separating walls.

FIGS. 8–9. Enlargement of basal megaspore to form embryo sac mother cell.

FIGS. 10–14. Stages in formation of embryo sac.

FIG. 15. Pollen tube just after entering embryo sac.

FIG. 16. Fusion of polars before rupture of pollen tube: *s*, synergid; *e*, egg.

FIG. 17. Lateral discharge of pollen tube: *e*, egg; *t*, tube nucleus; *s*, synergids.

FIG. 18. Simultaneous double fertilization.

FIG. 19. Double fertilization with discharge of tube nucleus (*t*); *e*, egg.

FIG. 20. Fusion of male and endosperm nuclei.

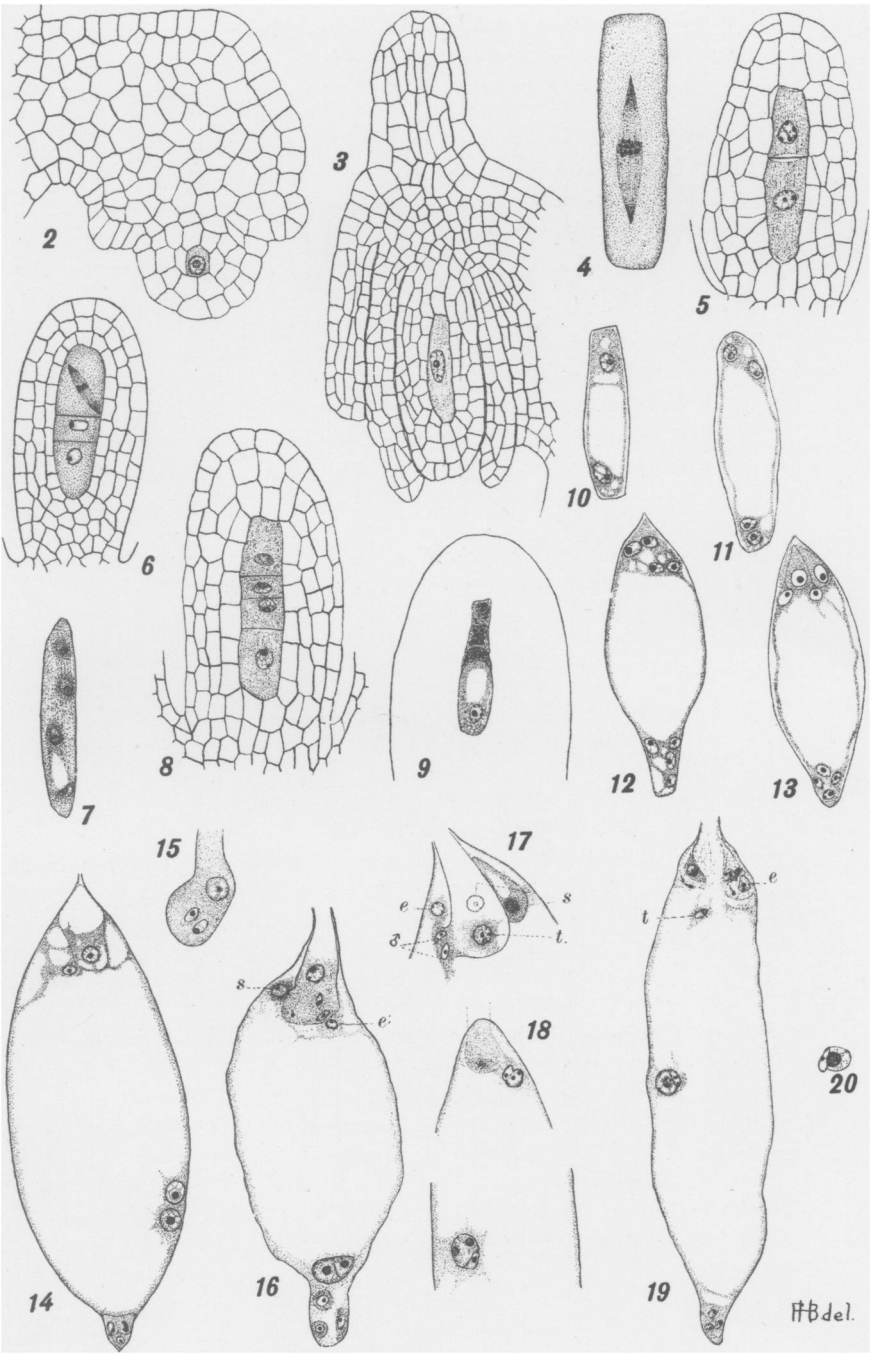
FIG. 21. Ovule at time of completed embryo sac.

FIG. 22. Elongation of ovule and outer integument after fertilization.

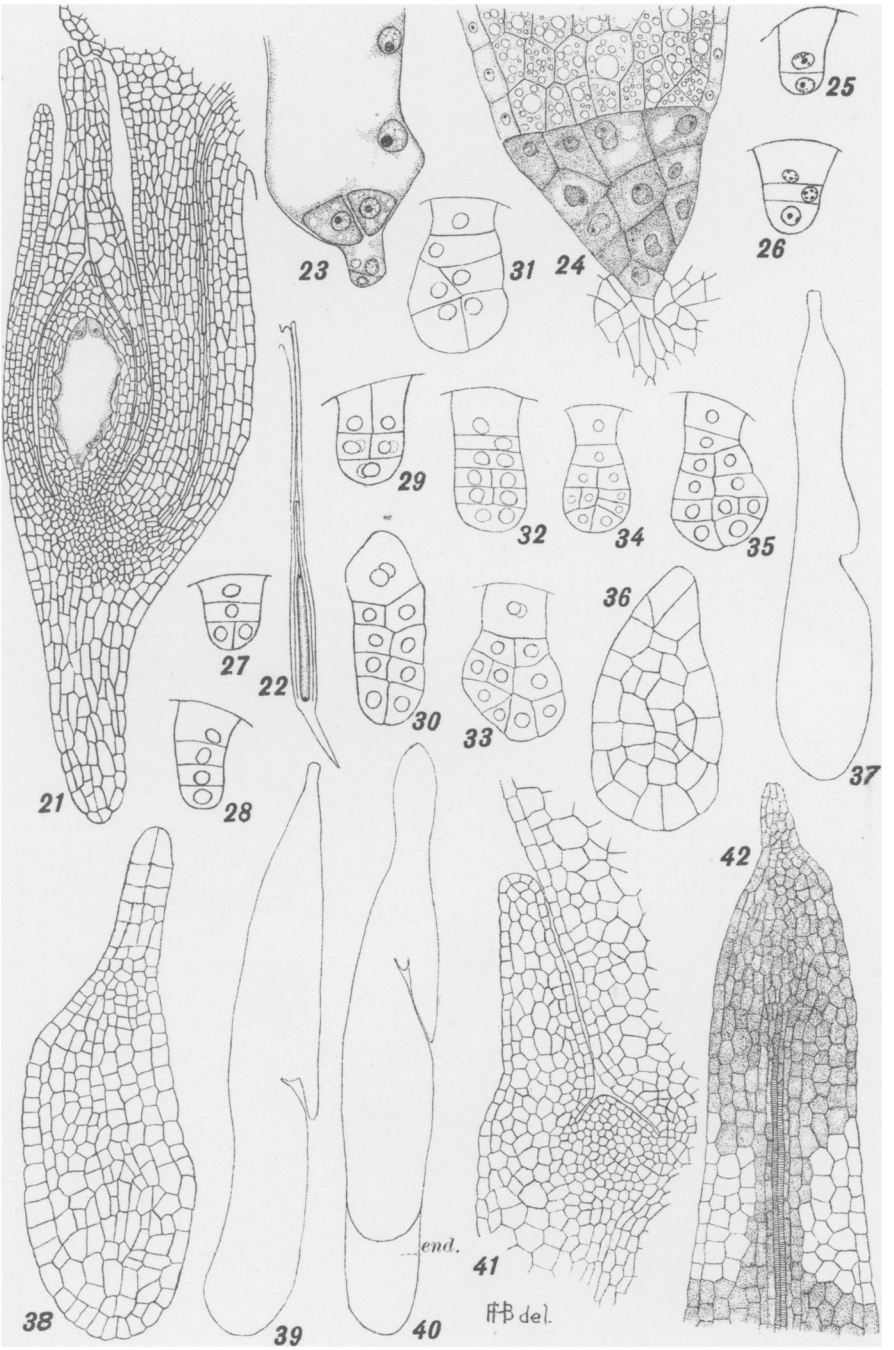
FIG. 23. First division in formation of chalazal endosperm tissue.

FIG. 24. Chalazal endosperm tissue and portion of endosperm that is to serve as reserve material in ripe seed.

FIGS. 25–26. Two- and three-celled embryos.



BILLINGS on TILLANDSIA.



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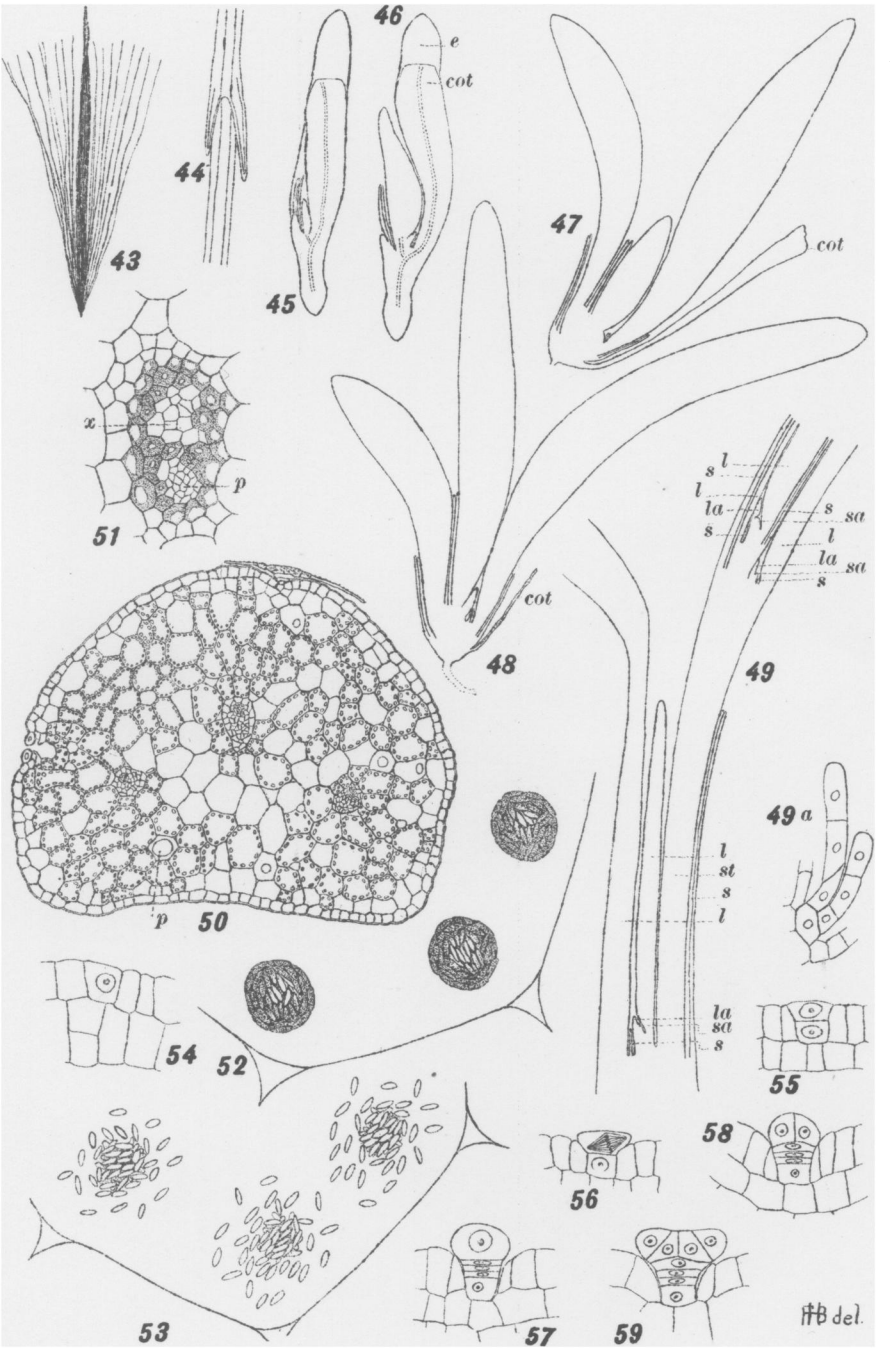

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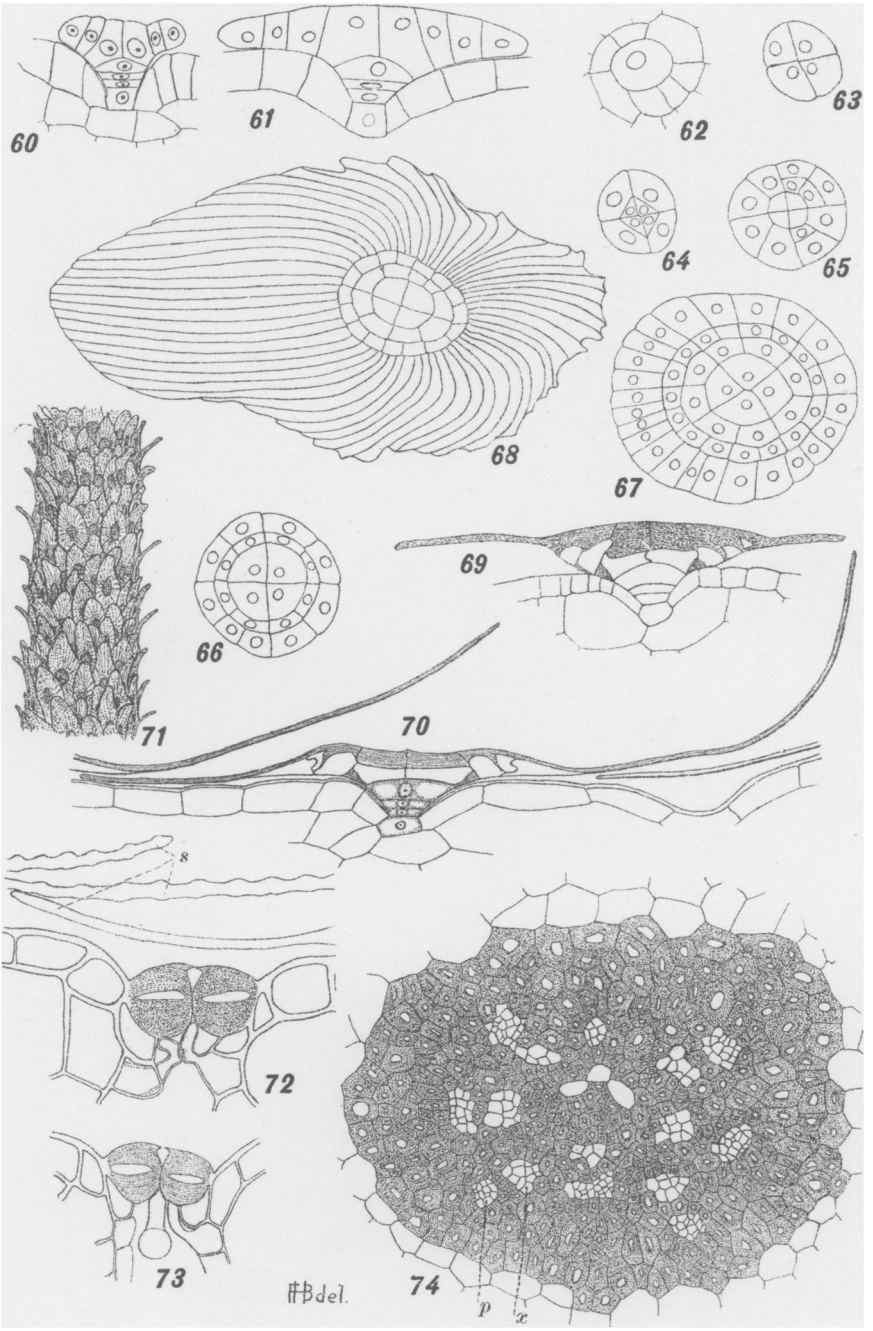

BILLINGS on TILLANDSIA.

FIG. 27. Formation of quadrant.

FIG. 28. Division of middle before terminal segment.

FIG. 29. Unusually early development of basal and middle segments.

FIG. 30. An unusual form of embryo.

FIGS. 31–36. Stages in embryo development; in *fig. 34*, the transverse walls in the terminal segment are oblique; the last three figures show beginning of dermatogen.

FIG. 37. Embryo about one-fourth grown.

FIGS. 38–40. Outlines of embryos in late stages of development; *fig. 30* represents a mature embryo.

FIG. 41. Region in vicinity of growing point of a nearly ripe embryo.

FIG. 42. Root region of nearly mature embryo, showing dead cortical cells.

FIG. 43. Ripe seed.

FIG. 44. Barbs on hair of coma.

FIG. 45. Early stage in germination; outline of longitudinal section.

FIGS. 46–48. Stages in development of seedling; outline of longitudinal section.

FIG. 49. Longitudinal section through the growing point regions of a mature plant: *s*, sheath; *st*, stem; *l*, leaf; *sa*, stem apex; *la*, leaf apex.

FIG. 49a. Very young sheath.

FIG. 50. Cross section of leaf; *p*, pit in water-storage cell.

FIG. 51. Bundle of leaf enlarged to show phloem (*p*) and xylem (*x*).

FIG. 52. Megachloroplasts showing division into microchloroplasts.

FIG. 53. Stage in separation of microchloroplasts by which they become distributed through the cytoplasm.

FIGS. 54–61. Stages in development of the scale seen in longitudinal section; *fig. 54* shows the epidermal cell from which the scale arises.

FIGS. 62–68. Stages in scale development seen from the surface; *fig. 68* shows a mature scale.

FIG. 69. Scale in longitudinal section, after soaking in water for several hours; the wing is seen to be raised considerably above the epidermis.

FIG. 70. Scale in longitudinal section, drawn from a paraffin section; it will be seen to lie much closer to the epidermis than the one in *fig. 69*.

FIG. 71. General appearance of the surface of the leaf, showing the scales.

FIG. 72. Section through a stoma; the guard cells are unquestionably closed; in addition a process has grown up from the parenchyma into the pore of the stoma; *s*, scales.

FIG. 73. Section of stoma showing slight variation from that in *fig. 72; figs. 72* and *73* were drawn from sections through living material.

FIG. 74. Cross section through the vascular region of the stem: *p*, phloem; *x*, xylem.